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Hominoid Primates from a New Miocene Locality Named Meswa Bridge in Kenya

The remains of a species of *Proconsul* from early Miocene deposits at Meswa Bridge are described. Associated dental, mandibular, maxillary and cranial specimens represent several immature individuals. They are equivalent in size to *Proconsul nyanzae* but differ morphologically, particularly in the greater breadth and degree of flare of the deciduous and permanent molars, but lack of adult individuals from Meswa Bridge makes it difficult to compare them adequately with existing species. They are therefore left unassigned as an indeterminate species of *Proconsul*.

1. Introduction

Excavations were begun in 1979 at Meswa Bridge, an Early Miocene locality in the Muhoroni Agglomerates at the base of the Koru sequence in western Kenya. Towards the end of the first field season some isolated teeth and a frontal bone of a hominoid primate were found, and during subsequent preparation of blocks of matrix an immature mandible was also recovered. The frontal bone has since been cleaned and reconstructed by Dr Alan Walker. In 1980 we continued the excavation and found an immature half-maxilla which may belong to the same individual as the frontal and mandible. A second and possibly a third individual of the same species is also represented in the deposits by more fragmentary specimens. In general the specimens are relatively complete and undistorted as are most from this site. The fossiliferous sediments accumulated as an infilling of an ephemeral channel in fluvial sands (Pickford & Andrews, 1981).

2. Maxilla

The material consists of an immature right maxillary fragment (KNM-ME 9) with dc and dp^3-dp^4 and a germ of P^3 , and a dentally older fragment from the left side (KNM-ME 11) containing the complete deciduous dentition and fully erupted M^1 . KNM-ME 4, an isolated right M^1 is morphologically identical to ME 11 and is probably its antimere. There is also an isolated M^2 (KNM-ME 19) which is consistent in size and morphology with the M^1 of ME 11 and which has tiny wear facets indicating that it may have completed eruption (Plate 1).

A conspicuous feature of the maxilla is its massiveness relative to the teeth. The lateral surface of the maxilla is inflated, particularly around the deciduous canine, and the teeth appear tiny in contrast. The deciduous incisors are low and robust, with large lingual

cingula, but the deciduous canine is more gracile. The dp^3 is a bicuspid triangular tooth and is unmolarized, whereas the dp^4 is a broad molariform tooth. The lingual cingulum on both teeth is small but the buccal and lingual surfaces of the crown both flare strongly and the roots are correspondingly splayed, more so than is usual even in deciduous teeth. The P^3 germ is fragmentary but is morphologically similar to previously described *P. nyanzae* and *P. major* specimens, and although the crown is incompletely formed it is clearly a smaller tooth than is usual for *P. major*. The M^1 is also strongly flared resulting in the tooth being relatively broad at the crown base (Figure 1). The lingual cingulum is again narrow. The protoconule is large and the mesial fovea restricted. The M^2 is similar in morphology to the M^1 except that the occlusal ridges and the lingual cingulum are more strongly developed.

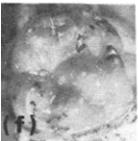
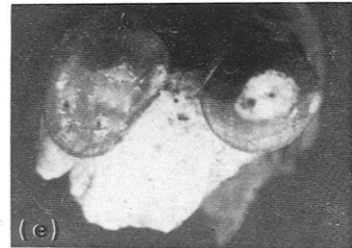
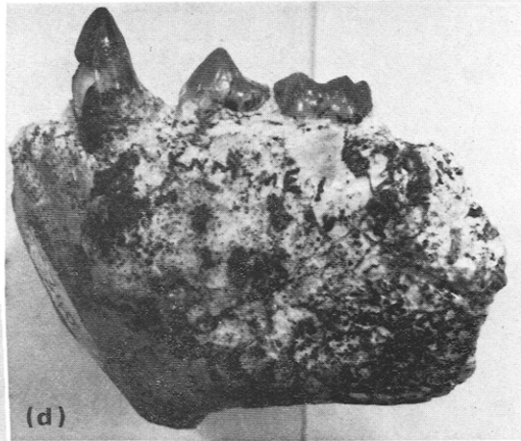
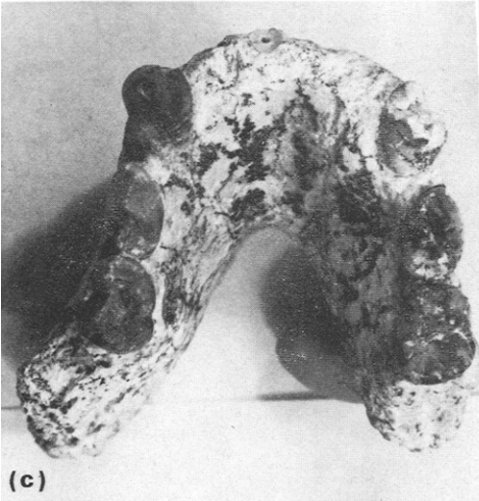
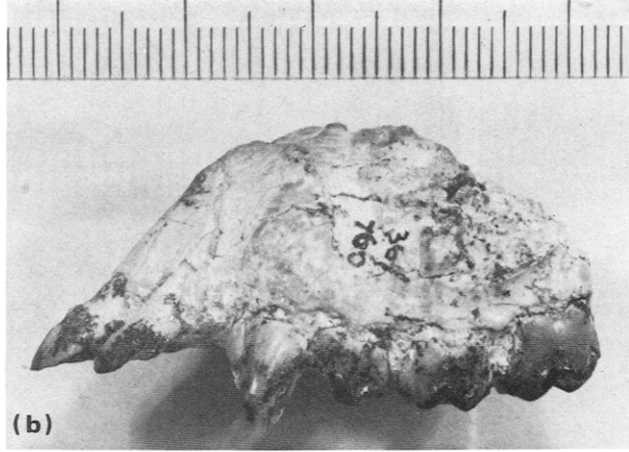
Dimensions of the upper dentition are given in Table 1. The Meswa Bridge permanent teeth are most nearly equivalent in size to *Proconsul nyanzae* (see Andrews, 1978). The deciduous teeth are relatively bigger and are *P. major*-sized, although with both deciduous and permanent teeth it is difficult to make a straight comparison because of the differences in shape. The deciduous and permanent molars are all considerably broader than long, more so than is usual in most *Proconsul* specimens (Figure 1), and the great breadth is the result of the lateral flare of the side of the crown, a feature that is continued into the roots which are also more splayed than usual in *Proconsul* species. In addition, the protoconule is prominent, the protocone is massive, and the mesial fovea is restricted: these are all characteristic of *Proconsul* but are more extremely developed on the Meswa Bridge specimens. In contrast to *Proconsul*, however, the lingual cingulum is less strongly developed.

Table 1

Dental measurements (mm)

		Mesiodistal length	Buccolingual breadth	Buccal height
<i>Maxillary teeth</i>				
KNM-ME 11	di^1	6.4	4.7	6.2
	di^2	4.4	3.6	6.2
	dc	6.6	6.2	9.4
(ME 9)	dc	6.6	5.8	—
	dp^3	6.7	8.6	5.1
(ME 9)	dp^3	6.2	7.3	—
	dp^4	8.2	10.6	—
(ME 9)	dp^4	7.3	8.7	—
	M^1	9.1	11.7	—
KNM-ME 19	M^2	10.2	12.5	—
<i>Mandibular teeth</i>				
KNM-ME 6	di_2	4.0	4.4	6.3
KNM-ME 8	dc	7.2	5.2	8.6
KNM-ME 1	dc	8.0	6.6	10.7
	dp_3	8.1	5.4	—
	dp_4	8.6	7.0	—
KNM-ME 10	dp_4	8.9	7.1	—
KNM-ME 3	M_1	9.3	8.1	—
KNM-ME 5	M_2	10.3	9.6	—
KNM-ME 7	I_1	5.4	4.0	10.5

Plate 1. Mandibular and maxillary specimens. (a) KNM-ME 11, occlusal view; (b) ME 11, lateral view; (c) KNM-ME 1, occlusal view; (d) ME 1, lateral view; (e) KNM-ME 9, occlusal view; (f) KNM-ME 5, occlusal view; (g) KNM-ME 19, occlusal view; (h) KNM-ME occlusal view; (i) KNM-ME 6, lingual view.



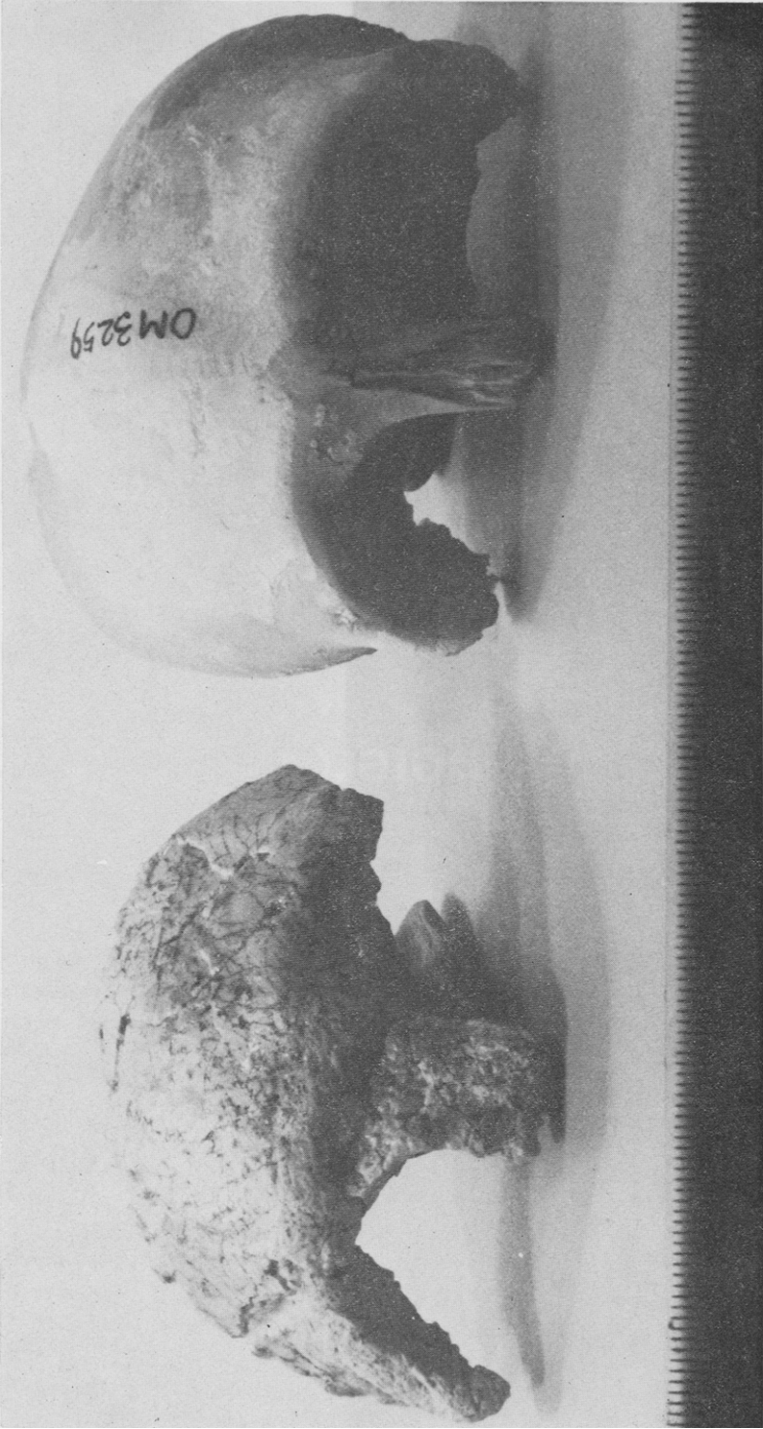
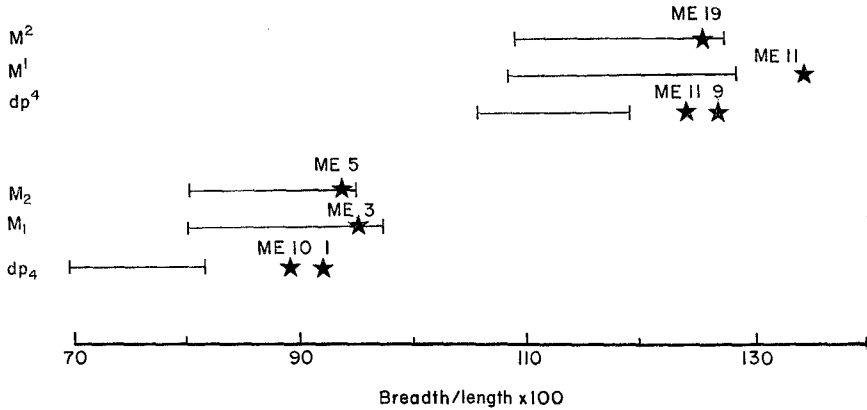


Plate 2. Frontal specimen, K.NM-ME 2, compared with an immature gorilla of approximately equivalent age.

Figure 1. Variation in molar breadth. The lines show the ranges of variation in the breadth/length index for three species of *Proconsul* combined (*P. africanus*, *P. nyanzae* and *P. major*) and the numbered stars denote the specimens from Meswa Bridge.



3. Mandible

The mandibular material from Meswa Bridge consists of an immature symphysis with both sides of the mandibular body intact (KNM-ME 1) and a number of isolated teeth (listed in Table 1). The mandibular body contains left dc, dp₃ and dp₄, and right dp₃ and dp₄, and this last tooth is duplicated by KNM-ME 10 which is also a right dp₄, showing unequivocally that at least two individuals are present in the deposits (Plate 1).

The mandibular symphysis is relatively deep, and has a superior transverse torus. There is no sign of an inferior torus. Like the symphysis, the mandibular bodies are deep, more so than on chimpanzees and *Proconsul* species of similar dental age, and this can be correlated with the high degree of inflation of the maxilla already mentioned. It may also be related to the degree of flare on the molars if this is considered to be a mechanism for increase in molar size.

There is no di₁ preserved. The di₂ is low crowned but with a relatively long root. The crown has a robust lingual pillar. A broken crown of a permanent central incisor is preserved which is extremely high crowned. The dc is high crowned, especially in ME 1, and has a low and small heel. This tooth is remarkably similar in size and morphology to the permanent canine of some *Proconsul africanus* specimens and must raise considerable doubt about the identification of some isolated *Proconsul* canines. The dp₃ is a single cusped tooth, although a small lingual cuspule is present as an outgrowth of a well developed lingual cingulum. The dp₄ is relatively short and broad with a wide talonid region and a rather long and narrow trigonid. The buccal cingulum forms a narrow but prominent ledge along the side of the crown. The occlusal ridges are sharply delineated and in contrast to the base of the crown the unworn occlusal surface is relatively narrow and elongated. The M₁ (KNM-ME 3) is a more rectangular tooth, relatively high crowned, and with a narrow buccal cingulum. The M₂ (KNM-ME 5) is similar to M₁ and both crowns are relatively broad, a characteristic also of dp₄ (Figure 1). The M₂ has an unusual development of a lingual "cingulum", producing two tubercles on either side of the metaconid.

The lower teeth are not as distinctive as the uppers and are more like those of other *Proconsul* species. The greater breadth of the molar crown is more like *P. major* than *P. nyanzae*, but the molars are significantly smaller than any known specimen of *P. major* and are beyond the 95% confidence limits for that species (Andrews, 1978). They fall into the lower half of the range of variation of *P. nyanzae*. The permanent I₁ (ME 7) is the size of a large *P. nyanzae* but it is very high crowned compared with *P. nyanzae*. The mandible is more gracile than in known specimens of *P. major* (e.g. KNM-SO 542), the inferior border is less inflated, and the symphyseal superior torus is smaller. In all of these characters the Meswa Bridge specimens are more like those of adult *P. nyanzae*. They differ from that species, however, in the breadth of the teeth and the relatively great depth of the mandible.

4. Skull

The greater part of an immature frontal bone (KNM-ME 2) is preserved, slightly distorted and reconstructed from a number of fragments (Plate 2). The upper borders of the orbits are relatively undistorted, and their conformation suggests a wide inter-orbital distance. If this reconstruction is correct it could be similar to the condition described for *Proconsul nyanzae* by Whybrow & Andrews (1978), but the interorbital region itself is crushed and the distance cannot be accurately measured. The supraorbital region has no torus, unlike the condition in *Pan* at a similar dental age but more like *Pongo*, assuming of course that the frontal bone is of similar age to the dental material described in the previous sections. Its absence at this stage of development makes it improbable that the adult condition developed a torus, and this is consistent with the lack of torus in *Proconsul africanus* (see Le Gros Clark & Leakey, 1951). The degree of postorbital constriction is greater than occurs in *P. africanus*, and the prominent temporal lines converge more closely together than is seen in *Pan* and again resemble the condition seen in *Pongo* more closely. They approach to within 4.5 cm of each other and are still converging at the broken posterior edge of the bone (Table 2). On the endocranial surface the sulcal pattern is remarkably similar to that described for *P. africanus* by Le Gros Clark & Leakey (1951).

Table 2

Skull and jaw measurements

	Specimen no.	Dimension (mm)
Maximum external breadth across the orbits	2	71.2
Orbit breadth	2	24.6
Maximum breadth across postorbital constriction	2	57.2
Depth of symphyseal cross-section	1	29.1
Thickness of symphyseal cross-section	1	13.9
Depth of mandibular body at dp ₄	1	24.5
Thickness of mandibular body at dp ₄	1	11.2
Internal breadth between maxillary dc	11	23.0
mandibular dc	1	17.1
maxillary dp ₄	11	20.6
mandibular dp ₄	1	22.0

The frontal bone, therefore, suggests similarities with comparable material of *Proconsul*, but, because it comes from an immature individual, and because there is so little comparable material, its taxonomic affinities are uncertain. Morphologically, however, it is of interest in showing great similarities to the *Proconsul africanus* skull despite the fact that it represents a rather larger species. The robusticity of the temporal lines correlates with the degree of inflation of the maxilla and with the deep mandible, while the breadth across the orbits and lack of supraorbital tori suggests a relatively broad and short face similar in shape to that of *P. africanus*.

5. Discussion

The Meswa Bridge sample of hominoids shows some degree of size variation (Table 1) but there is no indication that more than one species is present. The teeth are all morphologically compatible with each other, although the deciduous teeth are rather large in comparison with the permanent teeth: the deciduous teeth are equivalent in size to *P. major* specimens while the permanent teeth are closer to the *P. nyanzae* ranges of variation. The size of the permanent M1 and M2 suggests animals the size of *P. nyanzae* which had relatively larger deciduous teeth and in some cases (I_1 , dc) higher crowned teeth than in that species.

It seems likely that there are at least two and possibly three individuals present in the Meswa Bridge deposits. Several of the more complete specimens probably represent a single individual (consisting of specimens ME 1, 2, 4, 6, 11, 19). A second individual is represented by a number of specimens with smaller teeth and of slightly younger dental age (including ME 3, 8 and 9). The right dp_4 (ME 10) may also belong to this individual. The evidence for a third individual is based on the presence of a slight degree of wear on ME 5, a right M_3 which thus appears to be too old to fit into the first individual.

The affinities of the Meswa Bridge hominoids lie clearly with *Proconsul* species from the later deposits at Koru, Rusinga and Songhor, but the species identification is uncertain. The teeth are morphologically most like those of *P. major*, particularly in the relatively great breadth of the lower molars, both deciduous and permanent, but they are significantly smaller and are well beyond the 95% confidence limits of the *P. major* samples. In addition the upper and lower dp_4 's are relatively much broader than in *P. major* and the crowns of the upper cheek teeth have a greater degree of lateral flare and the roots are more widely splayed than is known for *P. major*. This is true of both permanent and deciduous upper molars. The mandibular body is relatively deeper and the symphysis is both deeper and has a smaller superior transverse torus than specimens of equivalent age of *P. major*.

Metrically the Meswa Bridge specimens are closest to *Proconsul nyanzae*, falling into the bottom half of the ranges of variation for that species. The molars of *P. nyanzae*, however, are slightly narrower than those of *P. major*, so that in terms of crown shape the Meswa Bridge specimens are further from *P. nyanzae* than from *P. major*. Neither of these species shows the lateral flare of the crown or the splaying of the roots of the upper molars described for the Meswa Bridge specimens. It does not seem possible, to assign these specimens to either *P. nyanzae* or *P. major*, especially in view of the uncertainty surrounding these species at present. As the Meswa Bridge species is currently represented only by immature specimens, they are referred here to an indeterminate species of *Proconsul* rather than being named a new species.

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